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GENETIC CONTROL OF EGG COLOUR POLYMORPHISM
IN *OPHRYOTROCHA PUERILIS SIBERTI*

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Riassunto. — Polimorfismo per il colore delle uova in *Ophryotrocha puerilis siberti*.

In una popolazione di *O. puerilis siberti* proveniente da Roscoff le uova sono gialle o bianche. Tale polimorfismo è determinato da un gene con una coppia di alleli, *Y* (giallo) e *y* (bianco), nella quale l'allele *Y* domina su *y*. Questo polimorfismo sembra avere un valore adattativo in quanto il tasso riproduttivo lordo degli incroci tra omozigoti gialli e bianchi risulta significativamente maggiore di quello degli incroci tra individui dello stesso genotipo.

Abstract. — In a population of *O. puerilis siberti* coming from Roscoff eggs show a yellow or white colouration. Such polymorphism is determined mainly by one locus with a pair of alleles (*Y* for yellow and *y* for white), the allele *Y* being dominant over the allele *y*. The hypothesis is advanced that such polymorphism has an adaptive value, as crosses between homozygous *YY* and *yy* individuals show fecundity rates significantly greater than those observed from crosses between homozygous individuals of the same genotype.

In natural populations of most species of the genus *Ophryotrocha*, polymorphism, as far as the outward appearance of the animal is concerned, is not an usual phenomenon. The first example of polymorphism in this genus has been reported by ÅKESSON (1977) in *O. diadema* for egg colouration. Recently in a population of *O. puerilis siberti* coming from Roscoff Aquarium a similar polymorphism for egg colouration was observed. In this species, as in *O. diadema*, eggs can be yellow or white, *i.e.* without pigment. The yellow colouration appears in the body of the animal, which is a protandrous hermaphrodite, at the beginning of the female phase, presumably when protogonia differentiate into nurse cells and oocytes.

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The present paper reports the results of genetic analysis of this polymorphism, as well as some preliminary observations, in order to establish if this polymorphism has an adaptive value.

Animals were reared at a constant temperature of 18°C in vessels containing 10 cc of filtered sea water with density of 0.026, and were fed with spinach. Matings were effected only between individuals showing oocytes, in order to be sure of their phenotype. It has already been known for a long time that in matings between two female phase individuals of *O. puerilis*, the one which has the biggest eggs (HARTMANN & LEWINSKI, 1940) or a stronger female genotype (BACCI & LA GRECA, 1953) brings about the reversal to the male phase of its partner. In some matings the sexual role remains fixed, in others each partner can change sex several times.

The F₁ progeny of crosses between animals coming from strains with yellow egg colouration and strains with white egg colouration, always produced yellow eggs. The offspring of 20 crosses between F₁ individuals consisted of 74.2% of yellow egg individuals and of 25.8% of white egg individuals (Table 1), a ratio which agrees with the theoretical 3:1 ratio, expected in a segregation of a pair of alleles of the same gene, the allele for yellow colouration *Y* being dominant over the one for white, *y*. Twelve back-crosses between F₁ yellow egg individuals and white egg individuals gave a 1:1 ratio of yellow egg to white egg individuals (Table 1), thus confirming the hypothesis that the character is under the control of one locus with two alleles.

TABLE 1.

	Offspring from 20 crosses <i>Yy</i> x <i>Yy</i>			Offspring from 12 crosses <i>Yy</i> x <i>yy</i>		
	phenotypes			phenotypes		
	yellow eggs	white eggs	total	yellow eggs	white eggs	total
observed	1176	409	1585	552	503	1055
expected	1188.75	396.25		527.5	527.5	
difference	—12.75	12.75		24.5	—24.5	
	χ^2	d.f.	P	χ^2	d.f.	P
total	5.148	20	0.99	2.275	12	0.99
pooled data	0.547	1	0.5	2.746	1	0.09
heterogeneity	4.601	19	0.99	0.512	11	0.99

A few preliminary observations were made on the values of some fitness parameters related to fecundity in three different series of crosses. The fecundity parameters taken into consideration are length of fertility life, *i.e.* the interval between the first and the last successful spawning of each couple, the reproductive rate, *i.e.* the mean number of fertilized eggs per couple per day, and the mean number of fertilized eggs per spawning.

At the moment, fecundity estimates of 14 *YY* x *YY* crosses, 10 *yy* x *yy* crosses and 20 *YY* x *yy* crosses are available (Table 2).

It is clear from the data of Table 2 that *YY* x *YY* crosses are the less fit and that the fecundity parameters of crosses between different genotypes are superior to those of both *YY* x *YY* or *yy* x *yy* crosses.

TABLE 2.
Mean values of fecundity parameters from different crosses
between *YY* and *yy* genotypes.

crosses	N	eggs/couple	spawnings/ couple	fertile life (days)	P	eggs/couple/ day	P	eggs/ spawning	P
<i>YY</i> x <i>YY</i>	14	302	3.7	47	n.s.	6.4	5%	81	2%
<i>YY</i> x <i>yy</i>	20	707	4.7	75.1		10.4		163	
<i>yy</i> x <i>yy</i>	10	471	4.3	61	2%	7.5	n.s.	101	5%

P is the probability of the observed Mann-Whitney statistics being equal or greater than its critical value.

Statistical analysis of these data by means of the non parametric Mann-Whitney U test (SOKAL & ROHLF, 1969) revealed no significant difference between the fecundity parameters of *YY* x *YY* and *yy* x *yy* crosses ($P > 0.2$). On the contrary, comparisons between fecundity estimates of either homogenotypic crosses and crosses between different genotypes show significant differences in the mean number of fertilized eggs per spawning. As far as the other two fitness parameters are concerned, differences between *YY* x *YY* and *YY* x *yy* crosses are always significant, while differences between *yy* x *yy* and *YY* x *yy* crosses do not reach the conventional level of significance.

These findings provide evidence that some kind of mutualistic interaction operates between individuals of different genotypes, at least for

fecundity parameters. Further research will prove whether other aspects of Darwinian fitness are correlated with yellow or white egg phenotypes and are subject to the same kind of interaction, and whether crosses between heterozygous individuals show heterosis.

Considerable evidence of various kinds of interactions among different genotypes occupying the same culture has been provided by a number of authors (see *e.g.*, besides authors quoted by SPIESS, 1977; BACCI & BORTESI, 1967; BRYANT & TURNER, 1972; FAVA, 1975; SEATON & ANTONOVICS, 1967).

The phenotypic interactions now observed in *O. puerilis siberti* are similar to those observed by BEARDMORE (1963) in experimental polymorphic populations of *Drosophila pseudobscura*, where there is a differential utilization of the same resources by different polymorphs.

According to WEISBROT (1966), the modification of the medium by biotic residues by each genotype acts either by complementing the nutritional requirements of the other genotypes (see *e.g.*, GUSTAFFSON, 1953; KEARSEY, 1965) or by inhibiting the development of the competing genotypes (see *e.g.* MATHER & MC GILL, 1972; FAVA, 1974) or through both mechanisms (DAWOOD & STRICKBERGER, 1969).

It should be particularly interesting to study the dynamics of egg colour polymorphism in both natural and experimental populations of *O. puerilis siberti*, in order to ascertain to which kind of selective forces it is exposed, even though the length of the generation interval in *O. puerilis siberti*, causes research programmes of this kind to be considerably troublesome.

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